

Notes on the pattern of head size in the Philippine Spotted Flying Lizard, *Draco spilopterus* (Weigmann, 1834), within Luzon Biogeographic Region, Philippines

Michael A. Tabug^{1,3}, Levy V. Necesito^{1,2}, Arvin C. Diesmos⁴

¹ The Graduate School, University of Santo Tomas, Manila 1015, Philippines

² Senior High School Department, University of Santo Tomas, Manila 1015, Philippines

³ Department of Natural and Applied Sciences, Isabela State University – Cabagan Campus, Garita Cabagan 3302, Isabela, Philippines

⁴ ASEAN Centre for Biodiversity, Biodiversity Information Center, Domingo M. Lantican Avenue, Los Banos, Laguna, Philippines

<https://zoobank.org/1F062A82-B948-4B08-813F-F8398D676D14>

Corresponding author: Michael A. Tabug (michaeltabug0507@gmail.com)

Academic editor: Yurii Kornilev ♦ Received 15 July 2022 ♦ Accepted 22 July 2023 ♦ Published 20 October 2023

Abstract

Sexual head dimorphism is a condition where head morphology of male and female of the same species differ, which provides an additional way to recognise sex for species identification. Fifty four adult Philippine Spotted Flying Lizards, *Draco spilopterus*, were examined from four populations in the Luzon Island, Philippines to assess whether head morphometry can drive sexual dimorphism. We identified the sex and measured five morphometric measurements of the head (jaw length, jaw width, head height, head length, head width) and snout-vent length. A univariate analysis of the five morphometric measurements showed clear sexual dimorphism. Considering all individuals, female heads are significantly larger than those of males (all p-values < 0.05). We also revealed major differences in head size amongst the four populations due to their geographical location and habitat differences.

Key Words

head size, flying lizard, Luzon Island, morphological variation, reptile

Introduction

In the traditional taxonomic classification of vertebrates, morphological characteristics are widely used for species identification. In lizards, morphological traits, associated with performance and dominance in competition and territoriality, are well-characterised (Wegener et al. 2019). For example, larger males of *Crotaphytus collaris* and *Anolis carolinensis* tend to be dominant over smaller ones and occupy larger territories (Jenssen et al. 2005; Lappin and Husak 2005). When males encounter equally-sized males of *Anolis cristatellus*, head shape and body size are the key predictors of the dominant behaviour (Perry et al. 2004).

Moreover, morphological traits are also examined to determine possible differences between males and females of species (sexual dimorphism), including the body size and shape, skin colouration and scale patterns (Cooper and Greenberg 1992; Adriana et al. 2005). Sexual dimorphism is commonly found within iguanid and agamid lizards (Stamps 1993). In some agamid *Draco* species, sexual dimorphism has been identified in dewlap size, patagial colouration and body size, wherein males have brighter and longer dewlaps, brighter and larger patagiums than females (Muster 1983; Mori and Hikida 1994; Shine et al. 1998), while females usually exhibit larger body size (Mori and Hikida 1994; McGuire and Alcalá 2000). In

contrast, Srichairat et al. (2016) revealed that males of *Draco maculatus* are larger than females with males having elongated and pointed dewlap. These two phenomena in sexual dimorphism can be attributed to varying levels of sexual differences related to evolutionary adaptations, such as sexual selection and natural selection (Stuart-Fox and Ord 2004; Srichairat et al. 2016).

More specifically, sexual head dimorphism is a condition where head morphology of male and female of the same species differ. Several studies were conducted in lizards to assess this condition (e.g. Scharf and Meiri 2013; Meyer et al. 2019; Cruz-Elizalde et al. 2020; Wang et al. 2020; Liang et al. 2022). Such research is limited in agamid *Draco* species (e.g. Srichairat et al. 2016), particularly to those that are endemic and widely distributed to the Philippines. Although the Philippine Spotted Flying Lizard (*Draco spilopterus*) has the widest geographic distribution, occurring on the Philippine Islands of Luzon, Marinduque, Polillo, Negros, Panay and Tablas (McGuire and Alcala 2000), little is known about potential sexual dimorphism within the species and amongst populations. Thus, the purpose of this study was to evaluate the head morphometric differences between males and females of *D. spilopterus* in the Island of Luzon in order to gain insight into their foraging behaviour and dietary pattern. Different populations of the flying lizard were also compared using the head morphometry as key predictor.

Materials and methods

Study species

The flying lizards of the genus *Draco* Linnaeus, 1758 (Family Agamidae, Subfamily Draconinae) are a unique group of agamid lizards, well-known for their ability to glide, utilising wing-like patagial membrane attached to their specialised thoracic ribs (McGuire and Alcala 2000; McGuire and Heang 2001; McGuire and Dudley 2011). *Draco spilopterus* can be diagnosed from other congeners in the Philippines by unique characteristics, such as lateral orientation of the nostrils, large size with a maximum snout-vent lengths of 85 mm and 97 mm in males and females, respectively, dorsal scales that are variable in size and often keeled or rugose, six ribs for patagial support, absence of lacrimal bone, absence of black postrectal ocellus, males with orange-yellow dorsal patagium and females with dark brown dorsal patagium with pale yellow mottling, ventral surface of patagium yellow for males, ventral surface of patagium brown for females, males with triangular lemon-yellow dewlap and both sexes having pale brown dorsal colouration (McGuire and Alcala 2000). However, there were no data on head morphometry that can be used in the diagnosis of *D. spilopterus* and in identifying the sex. Meanwhile, *D. spilopterus* feeds predominantly on a variety of insects and non-chitinous invertebrates, particularly ants, insect larvae and termites (Tabug et al. 2018; Tabug et al. 2020) which may drive variation in head morphometry.

Study sites

We conducted field sampling on Luzon Island, within the eponymous faunal region, a major biogeographic region in the Philippines, one of the centres of endemism in the country and amongst the oldest and the largest oceanic regions of the Philippine Archipelago. Luzon Island has an area of 104,688 km² and a roughly rectangular shape orientated in its longest axis north to south from 18°32'N to 12°31'N (Salita 1974; Vallejo 2014) (Fig. 1). This Island had a complex geological history and is considered as a product of the accretion of four paleo-islands (major mountains) during the Pleistocene (Hashimoto 1981; Auffenberg 1988; Hall 1998; Vallejo 2014). To the north are the Northern Sierra Madre and Central Cordillera mountain ranges, with Cagayan Valley situated in between and to the south and south-east lie the Southern Sierra Madre and Bicol Peninsula trending southeast for about 150 km and to the west large central plains and Zambales mountain ranges. Luzon Island has been surrounded by deep water and was never connected to other islands (Heaney et al. 2016). Due to a high degree of endemism across taxa, Luzon has been extensively studied for mammals (Heaney et al. 2016) and herpetofauna (Brown 1996; Diesmos 1998; Brown et al. 2012; Brown et al. 2013) and patterns of island biogeography (e.g. Brown and Alcala 1970; Heaney 2000). In addition, Luzon was suggested to have multiple lineages of widely-distributed flying lizards due to its geographic features and history (McGuire and Alcala 2000).

We selected four sites, based on museum locality data and published articles on the distribution of the Philippine Spotted Flying Lizard on Luzon (Brown 1996; Diesmos 1998; Brown et al. 2012; Brown et al. 2013). These sites were Ilocos, Laguna, Cavite and Bicol and were represented by their localities, namely Ilocos Norte Watershed, Mt. Banahaw, Mt. Palay-palay and Tapayas, respectively (Fig. 1).

Ilocos Norte Watershed (18°22'18"N, 120°38'49"E, datum WGS 84, 365 m elevation) lies at the northern edge of the Cordillera Central mountain range. This area is a human-modified environment dominated by commercially-important trees, such as mango, manila palm, coconut, star apple, gmelina tree and shrubs.

Mt. Banahaw (14°7'23"N, 121°28'8"E, datum WGS 84, 447 m elevation) is located in the southern part of Luzon Central Valley Basin. The Basin was formed between Southern Sierra Madre and Zambales Range which is composed of volcanic materials and sediments (Ku et al. 2009). In this area, *Draco* samples were collected within Barangay Bukal, Nagcarlan, Laguna. This barangay is dominated by Lanzones trees, coconuts, shrubs, mahogany and cultivated crops (banana). Ground cover included tall grasses, small ferns and leaf litters.

Mt. Palay-palay (14°13'54"N, 120°39'26"E, datum WGS 84, 311 m elevation) is situated within the Municipality of Nasugbu Batangas Province and Maragondon and Ternate, Cavite Province in a 4,000-hectare mountain

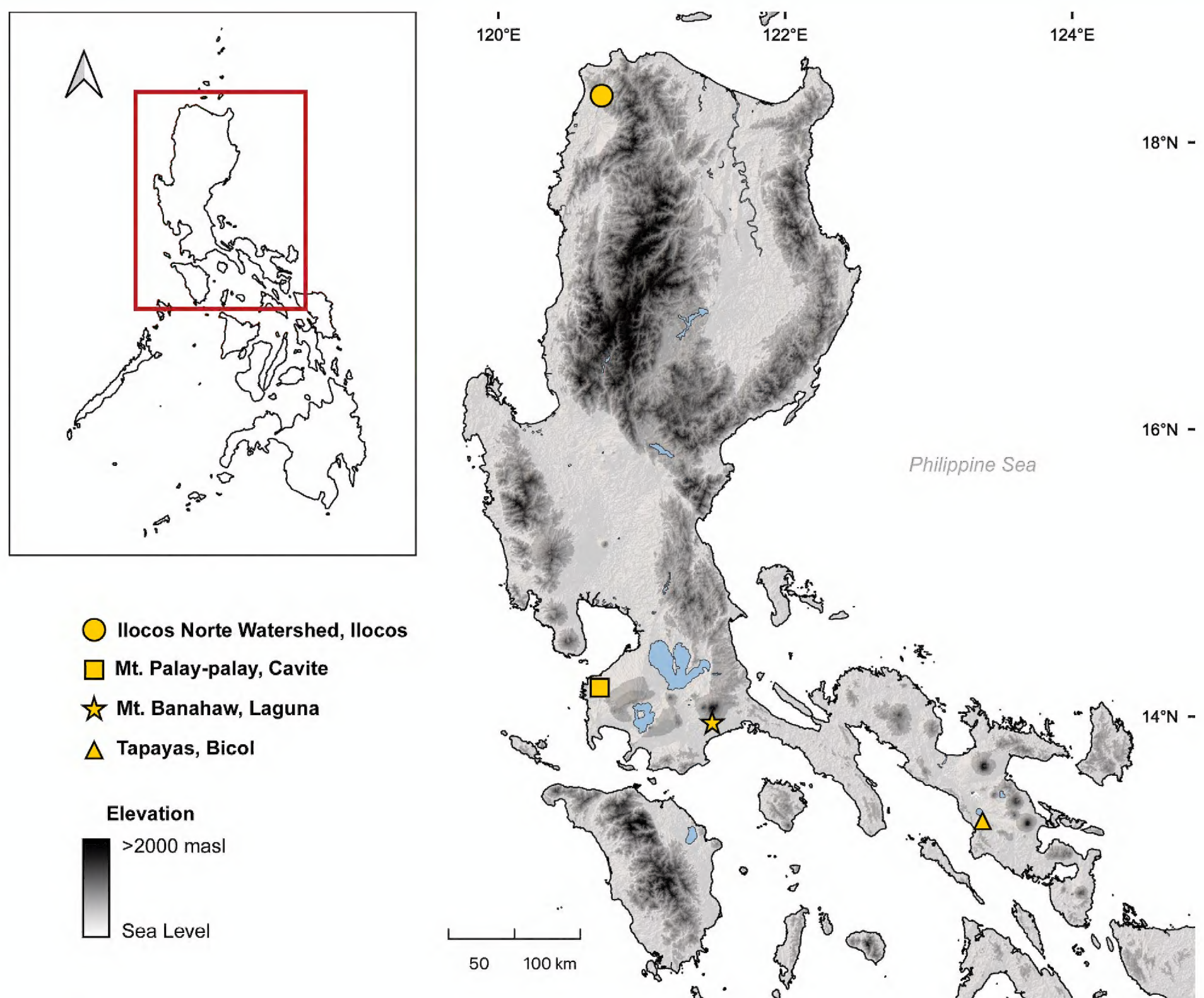


Figure 1. Sampling sites for *Draco spilopterus* on Luzon Island and general location of the island (mapped by YLC del Prado).

range (Luyon and Salibay 2007). The *Draco* samples were collected along the trails which are best-conserved forest. Bamboos are common along with the different trees, shrubs, leaf litters and fallen logs.

Tapayas (13°22'36"N, 123°16'8"E, datum WGS 84, 48 m elevation) is a village in the Municipality of Balatan, Camarines Sur Province in Bicol Peninsula. This area is located beside the rice field and creek and dominated by coconut trees. Mahogany and mango trees were also common along with small shrubs.

Sampling

We collected 54 adult individuals of *D. spilopterus* from four sites between June 2017 and March 2019. Collection of specimens was done 0700–1100 hr and 1400–1700 hr, which were the observed optimum periods of their foraging activity. In each study site, flying lizards were located by carefully searching each tree with the aid of binoculars (Mori and Hikida 1994). In capturing specimens, the technique described by Alcala (1967) and Mori and Hikida (1994) was adapted wherein a 7-m long pole with a

pliable tip was used to tap on the tree trunk at a point just above the perched lizard, in order to induce them to glide down either to the ground or to more accessible parts of trees for capture. Alternatively, a blowpipe loaded with plastic pellets was also used to catch flying lizards. We euthanised the specimens by immersion in dissolved chlorethane (McDiarmid 2011) immediately after capture. The following characters of the collected specimens were measured using a digital caliper (to the nearest 0.1 mm): snout-vent length (SVL; measured from the snout to the vent, jaw length (JL; measured from the back of the retro-articular process to the tip of the lower jaw), jaw width (JW; measured at the widest point of the jaw), head width (HW; measured at the widest part of the head), head length (HL; measured from the back of the parietal bone to the tip of the snout) and head height (HH; measured at the highest point of the head) (Fig. 2). We identified sex, based on the displayed patagial colouration on the live individuals and the dewlap: triangular lemon-yellow in males or small dark brown in females (Inger 1983; Musters 1983). The specimens were then fixed in 10% formalin and later preserved in 70% ethanol for long-term storage. All specimens (USTHRC vouchers ## 1311–1325,

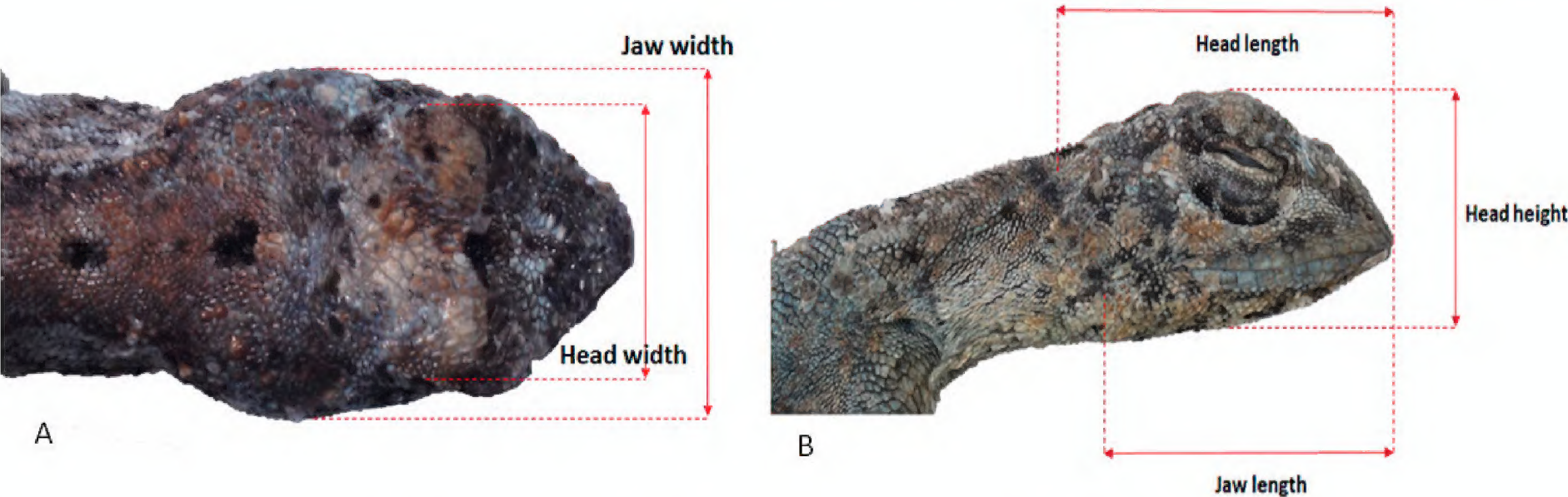


Figure 2. (A) Dorsal and (B) lateral view of the head of *Draco spilopterus* (Photo: LV Necesito).

1327, 1328, 1330–1366) were deposited at the Terrestrial Laboratory 707 of the Department of Biological Sciences at the University of Santo Tomas, Manila.

Head morphometric analysis

The SVL and head size variability between sexes and amongst *D. spilopterus* populations were quantified using morphometric characters. Log-transformed snout-vent length and head size variables were compared between sexes using t-test. One-way Analysis of Covariance (ANCOVA) was performed using log SVL (covariate) and log-transformed head-size variables (dependent variable) to determine the shared allometries amongst populations. When there is violation in the homogeneity of slope ($p < 0.05$), that is, differences in the rate of growth are detected, head size variables were size-corrected to standardise each individual to the same SVL and adjust measurements amongst populations using the technique of normalisation by Thorpe and Leonart (Thorpe 1976; Leonart et al. 2000) with the formula: $Y^* = Y_i(SVLM/SVLi)^b$, where Y^* is the size-corrected morphological features of the individual i , Y_i is the individual measurement of the morphological feature Y , $SVLM$ is the mean of snout-vent length of the

population to which the individual i belongs, $SVLi$ is the snout-vent length of the individual i and b is the slope of the linear regression between SVL and the morphological feature Y in the population (Van Kleeck et al. 2015). Principal component analysis in Paleontological Statistics (PAST) version 4.03 (Hammer et al. 2001) was performed on log-transformed size-corrected features to determine variables that contribute most to head size variation. Two-way ANOVAs were performed on principal component scores with highest eigenvalues to determine differences in head size in locality or sex. To further analyse the detected differences, Dunn’s post-hoc tests were used. We did linear regression analyses to each of the head measurement variables with snout-vent length (log-transformed).

Results

Sampled *D. spilopterus* varied in size from 55.16 mm to 98.31 mm SVL. Morphometric variation presented in Table 1 provides the range and mean of each population. The population from Laguna exhibited the largest body size. Ilocos population showed wider head dimensions both in males and females, while the Cavite population had the smallest body size and head dimension.

Table 1. Morphometric variation (mm) in mean and standard deviation of the SVL and head dimensions in each site. t-Test and ANCOVA (with SVL as covariate) of head dimension between sexes (pooled data of all sites). P-values with asterisk (*) are significant. Snout-Vent Length (SVL), Jaw Length (JL), Jaw Width (JW), Head Length (HL), Head Width (HW), Head Height (HH). Numbers in brackets indicate sample size.

	Ilocos		Laguna		Cavite		Bicol		Overall		t test	ANCOVA
	Male (6)	Female (3)	Male (11)	Female (4)	Male (15)	Female (3)	Male (8)	Female (4)	Male (40)	Female (15)		
SVL	75.9±10.7 55.16–84.22	80.89±5.37 74.69–84.23	81.85±8.86 73.94–92.27	83.86±15.74 59.9–98.31	71.32±5.03 58.23–78.19	66.78±2.84 64.65–70.00	71.89±4.01 65.19–77.56	75.62±10.44 62.30–86.60	75.01±1.18 55.16–92.27	77.65±3.08 59.9–98.31	0.148	-
JL	15.19±1.31 13.36–16.82	16.29±2.16 14.99–18.74	14.99±2.22 12.89–19.40	17.05±3.33 16.46–21.03	14.40±1.08 11.90–16.44	14.33±1.01 13.17–15.02	13.86±1.36 12.53–16.47	15.29±2.19 12.44–17.31	14.69±0.23 11.9–19.40	15.88±0.64 12.18–21.03	0.002*	0.031*
JW	9.71±0.21 8.38–10.65	12.08±0.99 10.94–12.70	9.46±1.50 8.67–12.90	11.34±2.61 10.01–13.66	8.81±0.86 6.96–10.00	9.64±0.61 9.07–10.28	8.93±0.38 8.24–9.41	10.29±1.92 7.78–11.80	9.22±0.16 6.96–12.92	10.87±0.50 7.56–13.69	0.002*	0.001*
HL	13.36±1.25 12.08–15.5	15.04±1.39 13.46–16.07	14.67±1.55 12.97–18.02	16.35±2.89 15.82–19.44	13.82±0.82 11.90–15.66	13.15±0.40 12.71–13.50	13.23±1.07 11.62–14.87	14.46±2.86 11.91–17.65	13.94±0.19 11.65–18.02	14.94±0.63 11.91–19.44	0.017*	0.046*
HW	10.06±0.53 9.34–10.95	11.92±1.39 10.88–13.50	10.07±0.96 9.66–11.84	11.08±1.13 10.25–12.50	9.18±0.83 8.01–11.09	9.67±0.51 9.26–10.24	9.06±0.74 7.99–10.17	9.28±1.40 7.53–10.9	9.59±0.14 7.99–11.84	10.49±0.39 7.53–13.5	0.008*	0.009*
HH	8.42±0.56 7.79–9.03	9.66±1.03 8.90–10.83	8.58±0.95 7.14–10.15	9.14±1.63 7.93–11.19	7.97±0.90 6.30–9.75	8.08±0.60 7.56–8.73	7.68±0.47 6.84–8.18	8.29±0.60 7.46–8.89	8.17±0.14 6.30–10.15	8.81±0.31 7.43–11.19	0.015*	0.049*

Snout-vent length was not significantly different between sexes, pooled for all individuals (t-test: $P = 0.148$, $df = 1$). However, all head measurements in females was significantly larger than in males (t-test). ANCOVA, with SVL as covariate, supports these findings (all P -values < 0.05 ; Table 1).

Regression analyses of the head dimension variables strongly correlated with snout-vent length (log-transformed, all $P < 0.001$) (Fig. 3, Suppl. material 1). ANCOVAs revealed differences in the rate of growth in jaw length amongst populations, as indicated in lack of homogeneity in the slope ($P < 0.05$, $F = 47.04$, $df = 3$), which requires the size-correction method to normalise the variables.

The size-corrected log-transformed data were analysed using PCA to determine the sources of variation. Five principal components were generated, three of which (PC1, PC2, PC3) accounted for 92.9% of the total variation (Table 2). PC4 and PC5 were also included to ensure that results presented are conservative with the analyses, even though they made up 4.2% and 2.9% of the total variation. However, two-way ANOVA revealed that PC4 and PC5 were not statistically significant amongst popu-

Table 2. Results of the Principal Component Analysis on morphological variables (adjusted for SVL) of *Draco spilopterus* from populations in Luzon Region. Values in bold are the morphological gradients that highly contribute to the percentage of variance.

Variables	PC1	PC2	PC3
Jaw length	0.357	0.169	0.521
Jaw width	0.710	-0.638	-0.243
Head length	0.303	0.069	0.696
Head width	0.389	0.360	-0.349
Head height	0.354	0.656	-0.252
% of Variance	71.9	11.3	9.7

lations and between sexes and no interaction was detected (all P -values > 0.05 ; Suppl. material 2). Of these, the first three components were used and discussed.

The first component (71.9% of variance, all positive loadings) describes a morphological gradient, based on jaw width and head width (Fig. 4; Table 2). The second component (11.3% of variance) describes head height and jaw width. The third component (9.7% of variance) describes a gradient, based on jaw length and head length. A two-way ANOVA on scores of the first three principal components revealed significant

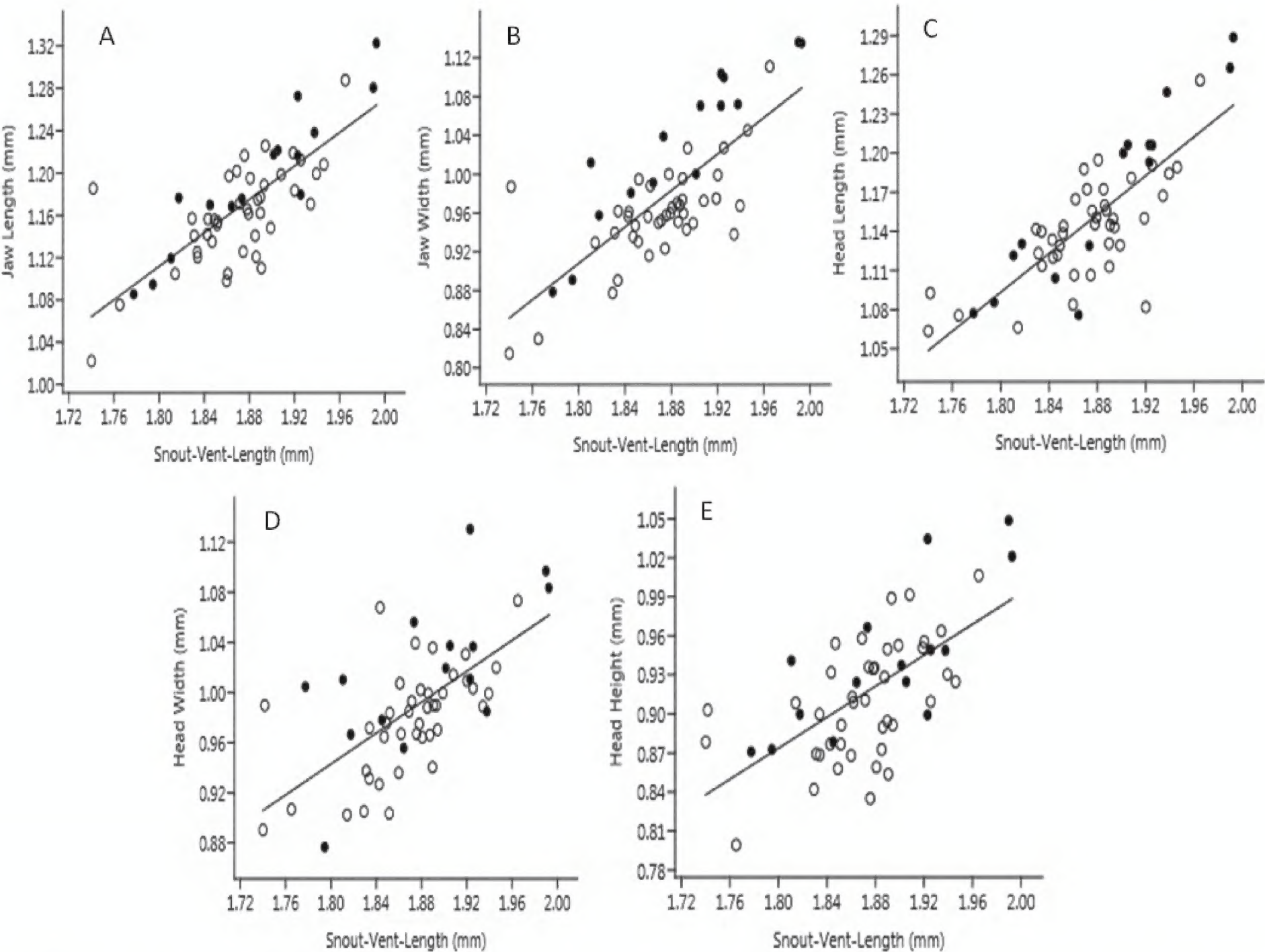


Figure 3. Dispersion diagrams from linear (Pearson's) correlations between **A.** Snout-vent length and jaw length ($r = 0.776$, $P < 0.0001$); **B.** Snout-vent length and jaw width ($r = 0.750$, $P < 0.0001$); **C.** Snout-vent length and head length ($r = 0.797$, $P < 0.0001$); **D.** Snout-vent length and head width ($r = 0.644$, $P < 0.0001$); **E.** Snout-vent length and head height ($r = 0.639$, $P < 0.0001$), of male (white dot) and female (black dot) of *Draco spilopterus*.

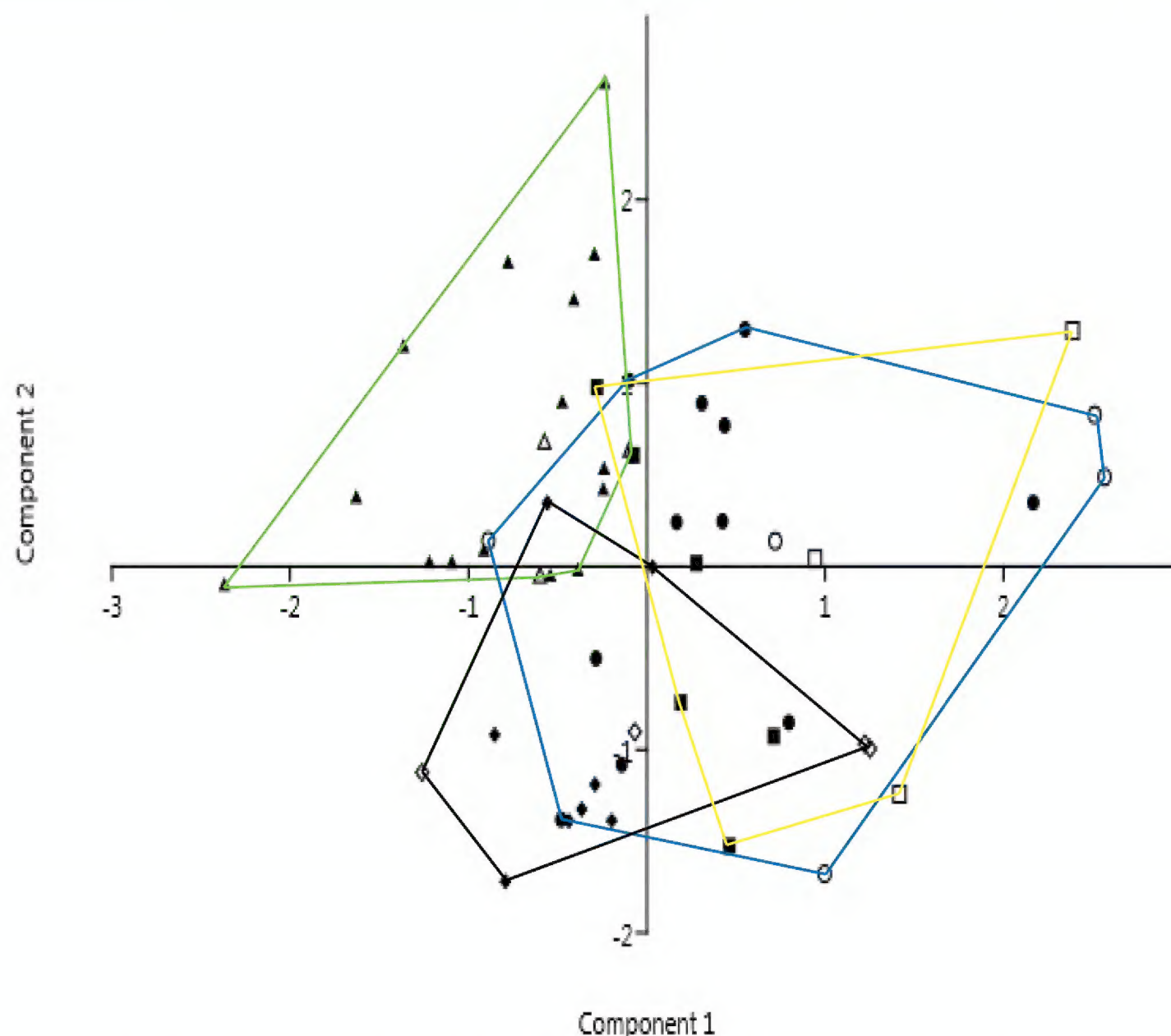


Figure 4. Principal Component Analysis scatter plot of head dimensions of *D. spilopterus* from four populations. (black dot) Mt. Banahaw, Laguna; (black diamond) Tapayayas, Bicol; (black square) Ilocos Norte Watershed, Ilocos; (black triangle) Mt. Palay-palay, Cavite.

differences amongst populations (all P -values < 0.05 ; Suppl. material 2). Dunn's post-hoc tests were applied to determine the extent of the variation on each PC score. Ilocos and Laguna populations had higher PC1 scores than flying lizards from Cavite and Bicol (post-hoc P -values < 0.05 ; Suppl. material 3). Individuals from Bicol had lower PC2 scores than those from the other populations (post-hoc P -values < 0.05 ; Suppl. material 3). Populations from Cavite and Ilocos had the highest and lowest PC3 scores, respectively. Moreover, variation has been observed in plots of principal components (Fig. 4).

Discussion

In most agamid species, females have smaller body and head size than males, even when corrected for body size (Lappin et al. 2006). This was supported in *Draco maculatus*, wherein males were larger than females, based on the snout-vent length, head length, head depth, mouth length and dewlap length (Srichairat et al. 2016). However, our results revealed that males have smaller head size than females for *D. spilopterus*. Shine et al. (1998) emphasised that the small head size of male *Draco* lizards is an adaptive character related to the maximal extension of the large dewlap used for social displays. Moreover, Mori and Hikida (1994) and Shine et al. (1998) hypothesised that the larger body and head size

of female *Draco* lizards is due to social and environmental interactions, such as less requirement for higher activity temperature, no territorial display and decreased gliding manoeuvrability.

Geographic variation in body size and head dimension in *Draco* has not been widely explored. As suggested by our results, even geographically close populations of a widespread lizard, *D. spilopterus*, can still vary morphologically. For instance, lizards from Cavite and Laguna, which are both located in south-central Luzon, show significant differences in head dimensions. Most interestingly, the lizards from Ilocos and Laguna, which are geographically distant populations, exhibit no significant differences in head dimension. Possibly, since the body size of lizards is tightly linked to their ecology (Miles 1994), the head variation amongst populations may be due to the effect of environmental factors that include diet composition, food availability and vegetation type (Boback 2006; Liang et al. 2022). The morphometric data presented in the study could be used as a supporting tool in studying other species of the remarkable group of flying lizards in the Philippines.

To further understand the sexual head dimorphism in *D. spilopterus* and head morphometric variation amongst its populations, we recommend an extensive assessment on the aspects of foraging behaviour, prey composition and size (e.g. natural selection) and bite force (e.g. sexual selection).

Acknowledgements

We are thankful to the Department of Science and Technology-Science Education Institute (DOST-SEI) through the Accelerated Science and Technology Human Resource Development Program (ASTHRDP) for the financial support. We are grateful to the National Geographic Society Young Explorer for the research fund. We thank the Philippine Department of Environment and Natural Resources for granting us the Gratuitous Permits (No. 277 and No. 2017–03) approved by the Protected Area Management Board of Ilocos Norte Watershed and Northern Sierra Madre. We thank the Municipal Environment and Natural Resources Office of Majayjay, Laguna for allowing us to conduct field sampling. We are grateful to M.V. Kleeck-Hann for suggesting appropriate statistical analyses and comments in this study, as well as two anonymous reviewers.

References

- Alcala AC (1967) Population biology of the “flying” lizard, *Draco volans*, on Negros Island, Philippines. *Natural and Applied Science Bulletin* 20(4): 335–372. <https://doi.org/10.2307/1442238>
- Adriana CS, Helga CW, Guarino RC (2005) Sexual dimorphism in the neotropical lizard, *Tropidurus torquatus* (Squamata, Tropiduridae). *Amphibia-Reptilia* 26(2): 127–137. <https://doi.org/10.1163/1568538054253384>
- Auffenberg W (1988) Gray’s monitor lizard. Gainesville: University of Florida Press, 419 pp. <https://doi.org/10.2307/1445749>
- Boback SM (2006) A morphometric comparison of island and mainland boas (*Boa constrictor*) in Belize. *Copeia* 2006(2): 261–267. [https://doi.org/10.1643/0045-8511\(2006\)6\[261:AMCOIA\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2006)6[261:AMCOIA]2.0.CO;2)
- Brown RM (1996) Amphibians and reptiles of the Zambales mountains of Luzon Island, Republic of the Philippines. *Herpetological Natural History* 4(1): 1–22. <https://doi.org/10.15560/8.3.469>
- Brown RM, Alcala AC (1970) The zoogeography of the herpetofauna of the Philippine Islands, a fringing archipelago. *Proceedings of the California Academy of Sciences* 38(1): 105–130. <http://biostor.org/reference/3125>
- Brown RM, Oliveros CH, Siler CD, Fernandez JB, Welton LJ, Buenavente PC, Diesmos ML, Diesmos AC (2012) Amphibians and reptiles of Luzon Island (Philippines), IV: Herpetofauna of Ilocos Norte Province, Northern Cordillera Mountain Range. *Check List* 8(3): 469–490. <https://doi.org/10.15560/8.3.469>
- Brown RM, Siler CD, Oliveros CH, Esselstyn JA, Diesmos AC, Hosner PA, Linkem CW, Barley AJ, Oaks JR, Sanguila MB, Welton LJ, Blackburn DC, Moyle RG, Peterson AT, Alcala AC (2013) Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution and Systematics* 44(1): 411–435. <https://doi.org/10.1146/annurev-ecolsys-110411-160323>
- Cooper WE, Greenberg JN (1992) Reptilian coloration and behavior. In: Gans C, Crews D (Eds) *Biology of the Reptilia: Hormones, Brain, and Behavior*. University of Chicago Press, Chicago, Illinois, USA, 298–422.
- Cruz-Elizalde R, Villamar-Duque TE, Ramirez-Bautista A (2020) Sexual dimorphism in size and shape in the viviparous lizard *Abronia taeniata* (Squamata: Anguinae) in central Mexico. *Acta Zoologica* 102(2): 220–226. <https://doi.org/10.1111/azo.12329>
- Diesmos AC (1998) The amphibian faunas of Mt. Banahao, Mt. San Cristobal, and Mt. Maquiling, Luzon Island, Philippines. Master’s Thesis, University of the Philippines at Los Banos College, Laguna, Philippines.
- Hammer O, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1): 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- Hashimoto W (1981) Geologic development of the Philippines. In: Kobayashi T, Toriyama R, Hashimoto W (Eds) *Geology and Palaeontology of Southeast Asia* 22: 83–170.
- Heaney LR (2000) Dynamic disequilibrium: A long term, large scale perspective on the equilibrium model of island biogeography. *Global Ecology and Biogeography* 9(1): 59–74. <https://doi.org/10.1046/j.1365-2699.2000.00163.x>
- Heaney LR, Balete DS, Rickart EA (2016) *The mammals of Luzon Island: biogeography and natural history of a Philippine fauna*. Johns Hopkins University Press, 94 pp.
- Inger RF (1983) Morphological and ecological variation in the flying lizards (genus *Draco*). *Fieldiana Zoology* 18: 1–35. <https://doi.org/10.5962/bhl.title.3131>
- Jenssen TA, Orrell KS, Lovern MB, Ross S (2000) Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia* 2000(1): 140–149. [https://doi.org/10.1643/0045-8511\(2000\)2000\[0140:SDIASS\]2.0.CO;2](https://doi.org/10.1643/0045-8511(2000)2000[0140:SDIASS]2.0.CO;2)
- Ku Y, Chen C, Song S, Iizuka Y, Shen JJ (2009) A 2 Ma record of explosive volcanism in southwestern Luzon: implications for the timing of subducted slab steepening. *Geochemistry, Geophysics, Geosystems* 10(6): 1–20. <https://doi.org/10.1029/2009GC002486>
- Lappin AK, Husak JF (2005) Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist* 166(3): 426–436. <https://doi.org/10.1086/432564>
- Lappin A K, Hamilton P S, Sullivan BK (2006) Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (= obesus)]. *Biological Journal of the Linnean Society* 88(2): 215–222. <https://doi.org/10.1111/j.1095-8312.2006.00615.x>
- Liang T, Wang L, Shi L (2022) Sexual selection and natural selection interplay in sexual head shape dimorphism of two sympatric race-runners (Squamata: Lacertidae). *Frontiers in Ecology and Evolution* 10: 1016885. <https://doi.org/10.3389/fevo.2022.1016885>
- Lleonart J, Salat J, Torres GJ (2000) Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology* 205(1): 85–93. <https://doi.org/10.1006/jtbi.2000.2043>
- Luyon HAV, Salibay CC (2007) Ectoparasites on murid rodents caught in Mts. Palay-palay/Mataas na Gulod National Park, Luzon Island, Philippines. *Southeast Asian Journal of Tropical Medicine and Public Health* 38(1): 194–202.
- McDiarmid RW, Mercedes S, Guyer C, Whitfield Gibbons J, Chernoff N (2011) *Reptile biodiversity: standard methods for inventory and monitoring*. University of California Press 1(2): 7–24. <https://doi.org/10.1525/9780520952072>
- McGuire JA, Alcala AC (2000) A taxonomic revision of the Flying Lizards (Iguania: Agamidae: *Draco*) of the Philippine Islands, with a description of a new species. *Herpetological Monographs* 14(14): 81–138. <https://doi.org/10.2307/1467046>
- McGuire JA, Dudley R (2011) The biology of gliding in flying lizards (Genus *Draco*) and their fossil and extant analogs. *Integrative and Comparative Biology* 51(6): 983–990. <https://doi.org/10.1093/icb/acr090>
- McGuire JA, Heang KB (2001) Phylogenetic systematics of Southeast Asian flying lizards (Iguania: Agamidae: *Draco*) as inferred from mitochondrial DNA sequence data. *Biological Journal of the Linnean*

- Society 72(2): 203–229. <https://doi.org/10.1111/j.1095-8312.2001.tb01312.x>
- Meyer JD, Irschick DJ, Vanhooydonck B, Losos JB, Adriaens D, Herrel A (2019) The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards. *Functional Ecology* 33(11): 2191–2202. <https://doi.org/10.1111/1365-2435.13438>
- Miles DB (1994) Covariation between morphology and locomotory performance in sceloporine lizards. In: Vitt LJ, Pianka ER (Eds) *Lizard ecology: Historical and experimental perspectives*. Princeton University Press, Princeton, 207–235. <https://doi.org/10.1515/9781400863945.207>
- Mori A, Hikida T (1994) Field observations on the social behavior of the Flying lizard, *Draco volans sumatranus*, in Borneo. *American society of Ichthyologists and Herpetologists (ASIH). Copeia* 1994(1): 124–130. <https://doi.org/10.2307/1446678>
- Musters CJM (1983) Taxonomy of the genus *Draco* L. (Agamidae, Lacertilia, Reptilia). *Zoologische Verhandelingen* 199(1): 1–120.
- Perry G, LeVering K, Girard I, Garland T (2004) Locomotor performance and social dominance in male *Anolis cristatellus*. *Animal Behaviour* 67(1): 37–47. <https://doi.org/10.1016/j.anbehav.2003.02.003>
- Salita DC (1974) Geography and natural resources of the Philippines. University of the Philippines System, Quezon City, Philippines, 53–65.
- Scharf I, Meiri S (2013) Sexual dimorphism of heads and abdomens: Different approaches to ‘being large’ in female and male lizards. *Biological Journal of the Linnean Society* 110(3): 665–673. <https://doi.org/10.1111/bij.12147>
- Shine R, Keogh S, Doughty P, Giragossyan H (1998) Costs of reproduction and the evolution of sexual dimorphism in a ‘flying lizard’ *Draco melanopogon* (Agamidae). *Journal of Zoology, London* 246(2): 203–213. <https://doi.org/10.1111/j.1469-7998.1998.tb00149.x>
- Srichairat N, Duengkae P, Jantrarotai P, Chuaynkern Y (2016) Sexual dimorphism in the spotted flying lizard *Draco maculatus* (Gray, 1845) (Squamata: Agamidae) from Thailand. *Agriculture and Natural Resources* 50(2): 120–124. <https://doi.org/10.1016/j.anres.2015.08.002>
- Stamps JA (1993) Sexual size dimorphism in species with asymptotic growth after maturity, *Biological Journal of the Linnean Society* 50(2): 123–145. <https://doi.org/10.1006/bijl.1993.1050>
- Stuart-Fox DM, Ord TJ (2004) Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B, Biological Sciences* 271(1554): 2249–2255. <https://doi.org/10.1098/rspb.2004.2802>
- Tabug MA, Necesito LV, General DEM, Diesmos AC (2018) Diet of *Draco spiloferus* from Ilocos Norte Province and Laguna Province, Philippines. *Southeast Asia Vertebrate Records* 30: 074–075.
- Tabug MA, Necesito LV, Diesmos AC (2020) *Draco spiloferus* (Philippine Spotted Flying Lizard). Diet. *Herpetological Review* 51(4): 848–850.
- Thorpe RS (1976) Biometric analysis of geographic variation and racial affinities. *Biological Reviews* 51(4): 407–452. <https://doi.org/10.1111/j.1469-185X.1976.tb01063.x>
- Vallejo B (2014) The biogeography of Luzon. In: Telnov D (Ed.) *Biodiversity, biogeography and nature conservation in Wallacea and New Guinea*. Germany: Latvian Society of Entomology 2: 47–59.
- Van Kleeck MJ, Chiaverano LM, Holland BS (2015) Prey-associated head-size variation in an invasive lizard in the Hawaiian Islands. *Biological Journal of the Linnean Society* 116(3): 626–636. <https://doi.org/10.1111/bij.12634>
- Wang XQ, Liang T, An J, Shi L (2020) Comparison of bite force performance and head shape between males and females of *Trapelus sanguinolenta*. *Chinese Journal of Zoology* 55(1): 29–36. <https://doi.org/10.13859/j.cjz.202001004>
- Wegener JE, Mulder KP, Pringle RM, Losos JB, Kolbe JJ (2019) Head size of male and female lizards increases with population density across island populations in the Bahamas. *Breviora* 566(1): 1–9. <https://doi.org/10.3099/0006-9698-566.1.1>
- Wiegmann AFA (1834) *Herpetologia Mexicana, seu descriptio amphibiorum Novae Hispaniae, quae itineribus Comitum de Sack, Ferdinandi Deppe et Chr Guil Schiede in Museum Zoologicum Bero-linense pervenerunt*. C. G. Liideritz, Berlin, Germany. <https://doi.org/10.5962/bhl.title.119131>

Supplementary material 1

Graphs of ANCOVA

Authors: Michael A. Tabug, Levy V. Necesito, Arvin C. Diesmos
Data type: TIF file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/herpetozoa.36.e90412.suppl1>

Supplementary material 2

Two-way analysis of variance of principal component scores

Authors: Michael A. Tabug, Levy V. Necesito, Arvin C. Diesmos
Data type: excel file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/herpetozoa.36.e90412.suppl2>

Supplementary material 3

Dunn's Post Hoc of PC1, PC2 and PC3

Authors: Michael A. Tabug, Levy V. Necesito, Arvin C. Diesmos
Data type: excel file

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/herpetozoa.36.e90412.suppl3>